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POPULATION AGE STRUCTURE, GROWTH AND LONGEVITY OF THE MARINE GASTROPOD *UROSALPINX CINEREA* SAY [1, 2]

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Urosalpinx cinerea Say is a West Atlantic temperate gastropod which is distributed on the North American coast from Nova Scotia to Nassau Sound, Florida. The species also occurs in the British Isles where it was probably introduced with consignments of the American oyster, *Crassostrea virginica* Gmelin (Orton, 1927). *U. cinerea* preys on a wide variety of marine invertebrates (Carriker, 1955; Wood, 1968) and in localities where the oyster is cultured, destruction of young oysters may be a serious commercial problem.

This species has been the subject of much research but information on its growth and longevity is incomplete, particularly for populations in North America. Information on the size of *U. cinerea* from different localities is available, notably the work of Cole (1942), Stauber (1943), Walter (1910), Federighi (1931a) and Myers (1965) and certain workers have attempted, unsuccessfully, to correlate size with temperature (Federighi, 1931b; Fraser, 1931). The problems involved in this type of correlation have been discussed by Carriker (1955) and Chestnut (1955).

The only detailed studies of growth of *U. cinerea* are based on populations from English waters (Cole, 1942; Hancock, 1959). Both authors assessed growth by size frequency analysis and Cole made use of growth interruption marks on the siphonal canal in evaluating the individual components of his polymodal size frequency curves. Andrews (1955) and others have commented that no evidence was provided to support the assumption that the interruption marks on the siphonal canal were annual growth marks (annuli). Andrews also noted that Cole's analysis lacks data on young *U. cinerea,* up through two years, owing to the difficulty in using an oyster dredge to collect small snails. Furthermore, Cole failed to provide evidence supporting his contention that the smooth curves fitted to the size frequency distributions represent year classes. Hancock's (1959) investigation included an analysis of size distribution of a population from the River Roach (Essex) as well as measurements of snails hatched and reared in the laboratory. By combining both sets of data, he was able to propose a cumulative growth curve for the population.

This investigation was undertaken to provide information on the age structure and growth of a North American population of *U. cinerea* (Southern New England) as a basis for future comparison with populations from other locations and ecological situations.

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Methods

The subject of this study is a population of *U. cinerea* from the Mystic River, near Noank, Connecticut. The habitat is a rocky intertidal shore formed by a railroad embankment. The snails occupy approximately the lower third of the littoral zone where they occur on the sides and undersurfaces of rocks. Because of its location just within the mouth of the Mystic River, this shore habitat is well protected from wave action. The yearly salinity range is approximately 29–31 ppt and the seasonal temperature range is from −1–25° C. Ice forms on the shore in late winter.

Sampling was begun in June 1967 but for reasons noted below, most of this study is based on material collected in October, 1968, plus six samples from May through October, 1969. A total of approximately 2500 oyster drills was used in this analysis. The method followed in collection of the snails was as follows: collecting began about 30 minutes prior to LW and was continued for one hour. All snails were collected by hand by picking snails from individual rocks. Every rock selected was examined carefully to be certain that all snails were removed, thus reducing sampling bias in favor of large snails. The same stretch of shore and the same vertical level was sampled each time. Snails were taken to the laboratory for measurement and returned to the sampling location, usually the same day. In October, 1969, a supplementary sample of only larger drills was taken in order to increase the sample size of snails older than one season.

Shell height (distance from the tip of the siphonal canal to the top of the spire) to the nearest 0.1 mm was measured with vernier calipers, but snails under 8 mm were measured with a calibrated stereomicroscope. In addition to shell height, the shell weights were determined for one sample (October 1969) as follows: the snails were treated with concentrated potassium hydroxide for one week, rinsed several times with tap water and flushed with a pasteur pipette, over dried overnight at 65° C and weighed to the nearest 0.01 g.

The method of determining growth and longevity in this study is by size frequency analysis of both shell length and weight. An attempt has also been made to interpret and correlate growth interruption lines on the shell with the size frequency data. Difficulties encountered in this type of correlation in Mollusca have been discussed by Haskin (1954) and Wilbur and Owen (1964). A particularly vexatious problem in *U. cinerea* is caused by the extended reproductive period and consequent large range in size of each year class. The extensive overlapping between year classes, in conjunction with the lower growth rates of older oyster drills, makes the identification of older year classes always difficult and sometimes impossible. In the present investigation the problem is reduced by the simultaneous analysis of both shell length and shell weight.

Results

Shell length frequency graphs for eight sampling dates beginning September 1967 are shown in Figure 1. The September 1967 population is polymodal but the lower peak, below about 8 mm, represents the 1967 year class which can be traced from its first appearance in the sample taken in July, 1967 (not shown). Sometime between September 1967 and the following June, an event important to the subsequent success of this study occurred, namely, the apparent disappearance of most of the 1967 year class. The cause remains unknown but the absence of this class is very evident in the June 1968 sample. The loss of most of this year class seems not to have seriously affected the population, as evidenced by the successful recruitment of the 1968 year class (Fig. 1, October 1968). The significance of the loss of the 1967 class becomes obvious in the May and June samples of 1969. In these, the total population is broadly bimodal. The lower

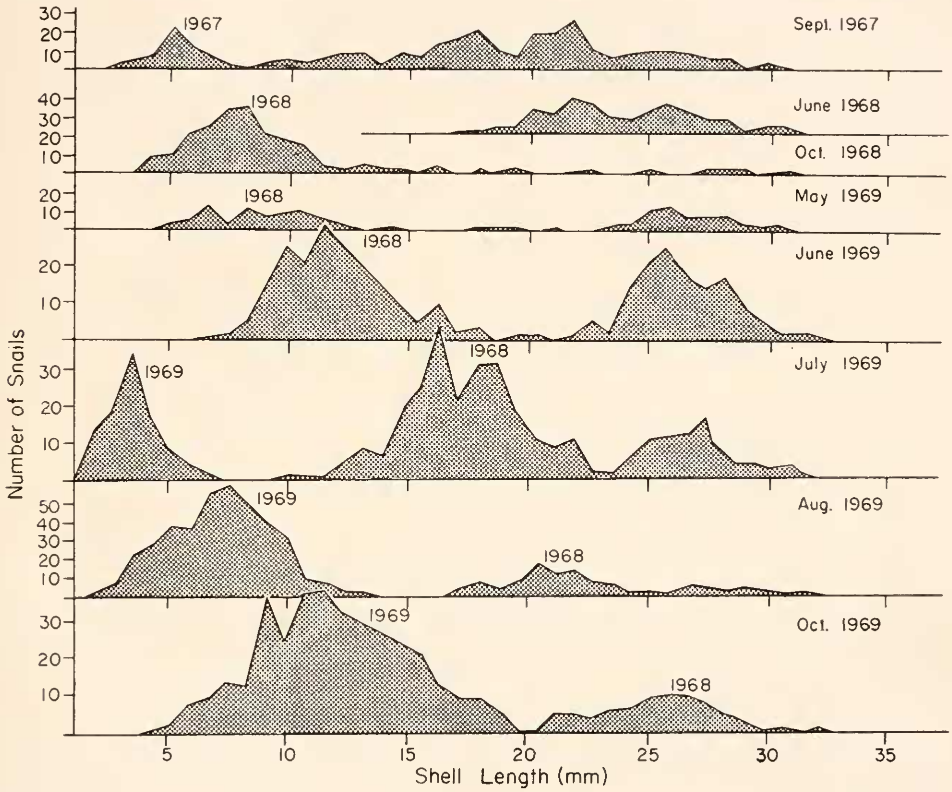

FIGURE 1. Size distribution of *Urosalpinx* from Noank, Connecticut, September 1967 through October, 1969. Numbers above the components of the distribution indicate the year of hatching.

(left) component clearly represents the previous (1968) year class; the upper component, a mixture of year classes including 1965 and 1966. The largely vacant space between these two components would have been occupied by the 1967 year class. Actually, a remnant of the 1967 year class is present and as shown below, can be demonstrated by the analysis of shell weight. In any case, the absence of most of the 1967 year class allows a more precise characterization of the 1968 class than would otherwise have been possible.

In the July sample, the 1969 year class makes its first appearance. By August, the entire population consists of three components, the new 1969 class at the left, the 1968 class occupying the center of the distribution, and a component of one or more year classes older than 1968 at the right. Note that beginning in May of 1969, the 1968 class is persistently polymodal although this was not evident the previous October. The reason for this is not known but since there can be no doubt that only a single year class is involved, this year class has been treated as a single unit.

Upgrowth of the 1969 class is evident in the July through October samples. Growth of the 1968 class also continues so that by October 1969, the 1968 class merges with the remnants of the older classes.

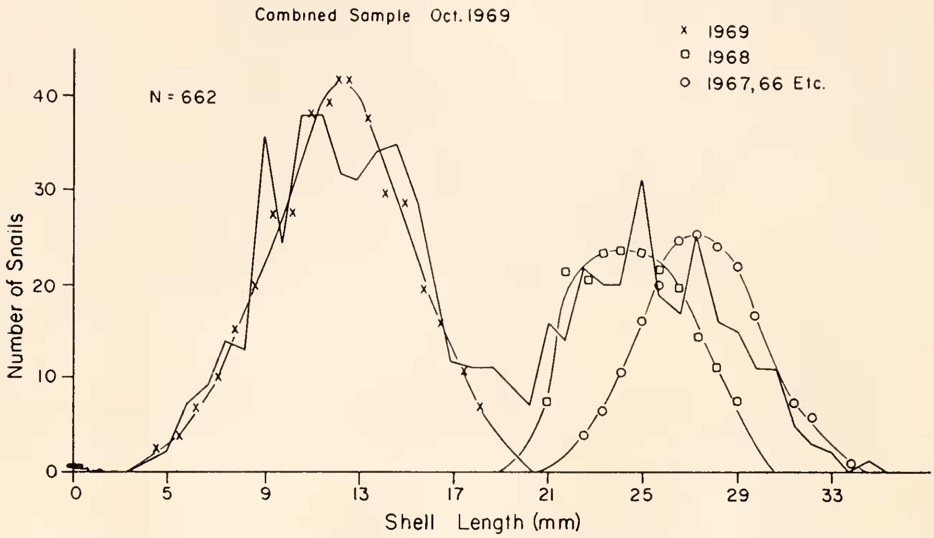

FIGURE 2. Size distribution of Noank *Urosalpinx*, pooled sample, October, 1969. Smooth curves have been fitted by the graphical "inflexion method" using normal probability paper (Lewis and Taylor, 1967).

Since the new class dominates the entire population in October 1969, a supplementary sample was taken the same day from which 1969 snails were excluded. Combined data from both of these samples is shown in Figure 2. The large component occupying the lower left of Figure 2 is unequivocally the 1969 year class. Using normal probability paper, this component was fitted with a smooth curve. The population component in Figure 2 above 20 mm is irregularly polymodal with two major peaks at 25 mm and 27.4 mm. Since this component must contain the 1968 class plus the population component representing the older classes, it is assumed that the peaks at 25 mm and 27.4 mm represent the modes of these two population components. Again, smooth curves were fitted to these two components. The three smooth curves of Figure 2 are postulations of the probably range, mode and degree of overlapping between the three population components present in the October 1969 sample. Two of these must correspond to the 1969 and 1968 year classes by virtue of their appearance and development in Figure 1. The third probably contains the remnant of the 1967 year class in addition to any older survivors.

The results of the shell weight analysis of the supplementary October sample are shown in Figure 3. The population is polymodal with at least four fairly well-defined components. These can be related to probable year class groups by comparison with Figure 2 and Figure 4, a double logarithmic regression of shell length and weight. The first component in Figure 3, with a mode of 0.22 g, includes oyster drills below about 20 mm and corresponds to the 1969 year class (some of which were inadvertently included in the supplementary October sample); the next component with a mode at 0.82 g corresponds to the 1968 year class; by a process of extrapolation, the third component probably represents the remnant of the 1967 year class. Figure 3 contains two further components, a larger with a major mode at 2.17 g which is interpreted as the 1966 year class,

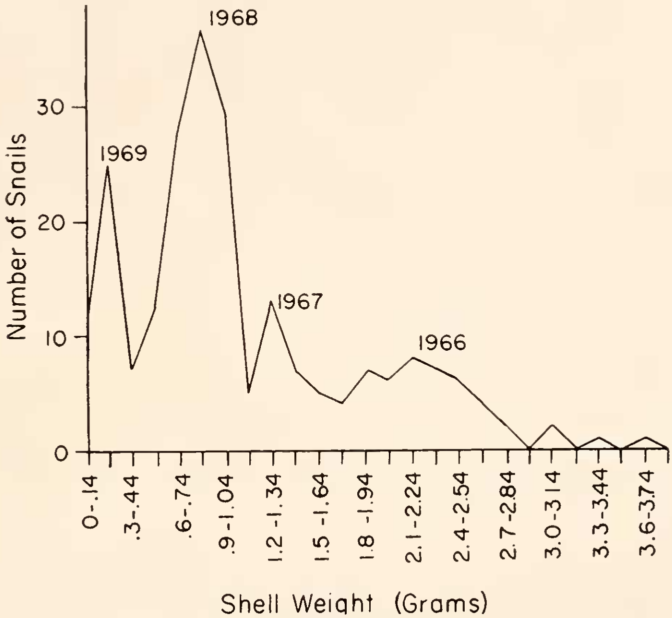

FIGURE 3. Shell weight distribution of supplementary 1969 sample. Numbers above the modes indicate the probable years of hatching.

and a smaller number of even larger snails which may or may not be survivors of an older year class. It is evident from Figures 2 and 3 that the analysis of shell weight permits the discrimination of several size components not evident from shell length frequency alone.

Growth annuli

To find supporting evidence for the growth data provided by the size analysis, the drills comprising the supplementary October 1969 sample were examined for the presence of annual growth interruption marks (annuli) on the shell, the underlying assumption being that snails examined in October at the end of their first growing season should lack annuli. Snails completing their second growth season should have a single annulus, after three seasons a second annulus should be present, and so on. The problem is to discriminate between a true annual growth interruption mark and a mark resulting from some other cause such as damaged outer lip. Consequently, the decision as to whether a mark is indeed a true annulus is highly subjective and in many cases impossible. Drills which were damaged or in which the cause of the interruption was in doubt were not included, so that data in Table 1 represent 168 out of an initial 224 snails.

It is evident from the table that there is a close correlation between the mean weight of snails in each of the first four growth mark categories and the mid-points of weight components believed to correspond to the 1966 through 1969 year classes (Fig. 3). The correlation between the range in weight of each of the

FIGURE 4. Double logarithmic plot of shell length and shell weight, pooled October 1969 sample. Curve is fitted visually.

growth mark categories and the range of their respective year class components is also close, with the exception of the group of snails with two growth marks. The excessive scatter in this group probably results from failure to discriminate between true and false annuli. This is particularly difficult in older drills because of erosion of the spire and partial masking by subsequent shell growth of a portion of the earlier annuli.

Cumulative growth

Figure 5 is a cumulative growth curve based on the analysis of both shell weight and length. When the cumulative shell length is plotted against age, the expected sigmoid growth curve is produced with a point of inflection near

TABLE I

Weight frequency data for U. cinerea *possessing growth annuli*

Midpoint of weight interval (grams) (Modal groups are italicized)	No. snails per growth interruption category				
	"0 marks"	"1 marks"	"2 marks"	"3 marks"	"4 marks"
0.07	7				
0.22	21	3			
0.37	3	3	1		
0.52	0	7	0		
0.67	2	21	3		
0.82	0	28	3		
0.97	1	16	7		
1.12		4	1		
1.27		5	5		
1.42		1	1	1	
1.57		2	2	0	
1.72		1	0	0	
1.87			1	1	
2.02			2	2	1
2.17			0	2	0
2.32			2	2	0
2.47			1	1	0
2.62				2	1
2.77				1	1
2.92					
3.07					
3.22					
3.37					
3.52					
3.67					
Mean weight (grams)	0.22	0.82	1.26	2.22	2.47

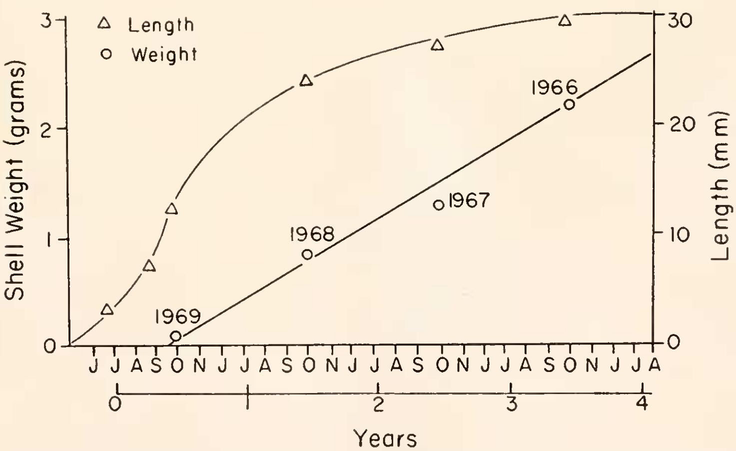

FIGURE 5. Cumulative growth curve for *Urosalpinx* from Noank, Connecticut. Letters stand for the months of the growth season, June through November.

the end of the first season, corresponding to the point of maximum growth rate. Close to seventy percent of the maximum shell length is attained by the end of the second growing season and little if any increase occurs after four years. The regression of shell weight on length approximates a linear function (Fig. 5), a characteristic which is shared by at least five other molluscan species (Sheldon, 1967). This author offered several possible explanations for this including the thickening of shell in older animals. In *U. cinerea* thickening of the outer lip occurs in older drills, as noted by Hancock (1959) and others.

Discussion

In general, the growth curve of Noank *U. cinerea* is similar to the River Roach (Essex) population reported by Hancock (1959), the only other population of the species for which comparable data are available. The population is comprised mostly of snails under 5 years of age and most of the shell growth occurs during the first two growing seasons.

The analysis of growth annuli provide evidence correlating these with size frequency. The usefulness of annuli in growth studies of *U. cinerea* is seriously hampered by the difficulty in discriminating between true and false annuli, especially when the latter are caused by damage to the outer lip early in the life of the snail. The growths marks discussed by Cole (1942) are useful but only in conjunction with growth annuli higher on the spire. Further studies using marked snails of known age would be helpful in delineating the variability in growth rates of the age classes as well as providing more precise information on population age structure.

One of the more interesting biological problems associated with growth of *U. cinerea* concerns the cause of the variation in maximum shell size which exists among populations. The most striking population in this regard occurs on the eastern shore of Virginia, particularly in Chincoteague Bay. The large size attained by individuals in this population is the basis for its designation as a subspecies, *U. c. follyensis* Baker (1951). However, even within the general range of shell size of *U. cinerea* there is considerable variability among populations. For example, there is some evidence that *U. cinerea* grows to a larger size in England than in North America (Fraser, 1931; Carriker, 1955; Cole, 1942) and on the Atlantic coast of the United States, significant variability occurs between populations (Fraser, 1931; Carriker, 1955; Cole, 1942).

While not excluding the significance of genetic factors in affecting maximum size, ecological factors acting on growth rate and the span of time during which growth continues are undoubtedly of great importance. These factors include the quality and quantity of available food and the length of the growing season. In the Noank population, remarkable year to year variability in mean shell size of the current year class is evident in the years 1968 and 1969 (Fig. 1). This variability seems to be related to certain ecological characteristics of this population.

Studies on the biology of *U. cinerea,* particularly those by Wood (1968), have shown that much of the biological success of this species can be credited to its capacity for utilizing a variety of prey species. The barnacle *Balanus balanoides* and the mussel *Mytilus edulis* are the major prey at intertidal habitats in the middle Atlantic region. At Noank, however, *Mytilus* is of no consequence as prey due to failure of this species to settle successfully at this site and there is no doubt that *B. balanoides* is the major prey. Predation on *B. balanoides* is intensive and snails in the process of attack have been observed many times, both in the field and laboratory. The barnacles settle in enormous numbers in the spring, usually March, so that a large prey population is already present when the snails emerge from dormancy in late April. Normally, however, only a single settlement of *B. balanoides* occurs so that predation by *U. cinerea* continually reduces a finite food supply. The age class of snails which most benefits from the large barnacle settlement is the previous year class, now in the second half of its first full year of life. The presence of a large food supply coinciding with a large component of the predator population capable of utilizing it may contribute to the high absolute growth rates which occur during the second half of the first year.

While *B. balanoides* is undoubtedly the major, and probably the preferred, prey species at Noank, it is not the only species preyed on by *U. cinerea*. Below LW, where barnacles are initially less dense than higher in the intertidal zone, the gastropod *Littorina littorea* is commonly attacked and it is not unusual to see several predators attacking a single *Littorina*. This may occur even when barnacles are available close by.

The encrusting ectoprocta, particularly *Cryptosula pallasiana* (Moll.), apparently occupy an important place in the ecology of *Urosalpinx* at this location. Although it is likely that all age groups feed to some extent on *Cryptosula*, newly hatched snails and snails still in their first season of growth are most frequently associated with the ectoprocts. This is understandable in view of the seasonal nature of the barnacle population. The latter settle in early spring. By the time the current year class of *U. cinerea* appears in July, the remaining barnacles ungrazed by older snails have grown significantly, decreasing their suitability as food for the newly hatched snails. The latter utilize the abundant supply of encrusting *Cryptosula*.

As noted by Wood (1968), it is unlikely that in the normal course of events *U. cinerea* ever completely decimates its supply of barnacles. However, there is also little doubt that as barnacles become less abundant due to grazing or other ecological factors, other species such as ectoprocts become increasingly more important as prey, especially in the lower portion of the intertidal zone. From an ecological point of view, this diversification in prey leads to a reduced competition for food within the population, *i.e.*, to a certain extent, newly hatched snails are not forced to compete directly with older members of the population for a single food supply. Although it is known that *U. cinerea* can undergo a normal, and even rapid, development in the laboratory when reared from hatching on a diet of oysters (Franz, 1966) or barnacles (Wood, 1968), ectoprocts occur abundantly virtually everywhere that *U. cinerea* is normally found. It would be interesting to determine if ectoprocts play a comparable role at other locations in the nurture of newly hatched *U. cinerea*.

Summary

1. A study of growth and age structure in a Connecticut population of *Urosalpinx cinerea* was carried out using both shell length and weight frequency analysis. A cumulative growth curve is proposed and compared with other published data for the species.

2. Growth interruption marks (annuli) occur in *Urosalpinx* but are not as useful as in some other mollusks because of difficulty in discriminating annuli from interruptions caused by other factors.

3. Close to seventy percent of maximum shell growth is attained after two growing seasons. No increase in length occurs after four to five years and older snails, if present, constitute a very small proportion of the total population.

4. Growth of oyster drills in their first season is highly variable. Prey quality and availability may be the principal cause of this.

5. At Noank, *Balanus balanoides* is the major prey species of *U. cinerea* but newly hatched and very young snails frequently attack encrusting ectoprocta, particularly *Cryptosula pallasiana*. This diversification of prey is an advantage to the predator since it leads to a reduction in competition for food between juveniles and adults.

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